anomaly. Releases made at places magnetically similar to our sites A, B, and C (his places 2 and 4) produced the same effect (FREI 1982, p. 136). But it should be pointed out that, in his 1982 paper, FREI argues that the general tendency to fly up the gradient in his experiments represents a particular case of a strategy which would induce a tendency to fly down the gradient when the field intensity at the home site is lower than at the release site (as in WAGNER's, 1976, experiments in the Chasseral anomaly, for instance). Applied to our mice, FREI's (1982) argument would imply that mice displaced from North to South in areas A and B, and from East to West in Area C should have their homing facilitated by a tendency to run down the gradient, which was apparently not the case. However, FREI's (1982) presentation of results is limited to vanishing bearings (at up to 3 km from release site) and does not differentiate among pigeons according to level of previous training and experience, which makes comparisons with our results more difficult.

Acknowledgements

Zusammenfassung

Heimfindeverhalten von Wald- und Gelbhalsmäusen (Apodemus) in einer geomagnetischen Anomalie

Die Hypothese, daß ein vorherbeschriebener „Richtungseffekt" im Heimfindeverhalten von wilden Mäusen durch eine lokale Störung des Erdmagnetfeldes verursacht war, wurde in einem Freilandexperiment geprüft. Der Heimkehrerfolg von insgesamt 440 an vier verschiedenen Stellen des magnetischgestörten Gebietes verfrachteten *Apodemus* stützt die Hypothese nur schwach. Die Ergebnisse zeigen nur nahe der Mitte zwischen den Orten größter magnetischer Intensität einen möglicherweise hemmenden Effekt auf den Heimkehrerfolg.

References

ANDERSON, P. K.; HEINSOHN, G. E.; WHITNEY, P. H.; HUANG, J. P. (1977): *Mus musculus* and *Peromyscus maniculatus:* homing ability in relation to habitat utilization. Can. J. Zool. **55**, 169–182.

AUGUST, P. V. (1985): Evidence for a magnetic compass in *Peromyscus leucopus.* Edmonton: IVth Intern. theriol. Congr., abstract 0035.

BAKER, R. R. (1981): Human navigation and the sixth sense. London: Hodder and Stoughton.

— (1984): Bird navigation: the solution of a mystery? London: Hodder and Stoughton.

BOVET, J. (1962): Influence d'un effet directionnel sur le retour au gîte des mulots fauve et sylvestre (*Apodemus flavicollis* Melch. et *A. sylvaticus* L.) et du campagnol roux (*Clethrionomys glareolus* Schr.) (Mammalia, Rodentia). Z. Tierpsychol. **19**, 472–488.

— (1965): Rôle des cours d'eau dans la limitation du domaine vital des rongeurs. Mammalia **29**, 452–462.

— (1978): Homing in wild myomorph rodents: current problems. In: Animal migration, navigation and homing. Ed. by K. SCHMIDT-KOENIG and W. T. KEETON. Berlin: Springer Verlag. 405–412.

— (1982): Homing behavior of mice: test of a "randomness"-model. Z. Tierpsychol. **58**, 301–310.

ETIENNE, A. S.; TERONI, E.; MAURER, R.; PORTENIER, V.; SAUCY, F. (1985): Short-distance homing in a small mammal: the role of exteroceptive cues and path integration. Experientia **41**, 122–125.

ETIENNE, A. S.; MAURER, R.; SAUCY, F.; TERONI, E. (1986): Short-distance homing in the golden hamster after a passive outward journey. Anim. Behav. **34**, 696–715.

FILDES, B. N.; O'LOUGHLIN, B. J.; BRADSHAW, J. L.; EWENS, W. J. (1984): Human orientation with restricted sensory information: no evidence for magnetic sensitivity. Perception **13**, 229–236.

FREI, U. (1982): Homing pigeons' behaviour in the irregular magnetic field of Western Switzerland. In: Avian navigation. Ed. by F. PAPI and H. G. WALLRAFF. Berlin: Springer Verlag. 129–139.

FREI, U.; WAGNER, G. (1976): Die Anfangsorientierung von Brieftauben im erdmagnetisch gestörten Gebiet des Mont Jorat. Rev. suisse zool. **83**, 891–897.

GOULD, J. L. (1982): The map sense of pigeons. Nature **296**, 205–211.

GOULD, J. L.; ABLE, K. P. (1981): Human homing: an elusive phenomenon. Science **212**, 1061–1063.

KEETON, W. T. (1974): The orientational and navigational basis of homing in birds. Adv. Study Behav. **5**, 47–132.

KIEPENHEUER, J. (1982): The effect of magnetic anomalies on the homing behaviour of pigeons: an attempt to analyse the possible factors involved. In: Avian navigation. Ed. by F. PAPI and H. G. WALLRAFF. Berlin: Springer Verlag. 120–128.

KOZEL, R. M.; FLEHARTY, E. D. (1979): Movements of rodents across roads. Southern Nat. **24**, 239–248.

KRAMER, G.; PRATT, J. G.; SAINT PAUL, U. V. (1956): Directional differences in pigeons homing. Science **123**, 329–330.

— — — (1958): Neue Untersuchungen über den „Richtungseffekt". J. Ornithol. **99**, 178–191.

LEDNOR, A. J.; WALCOTT, C. (1983): Homing pigeon navigation: the effects of in-flight exposure to a varying magnetic field. Comp. Biochem. Physiol. **76A**, 665–671.

MATHER, J. G. (1985): Magnetoreception and the search for magnetic material in rodents. In: Magnetite biomineralization and magnetoreception in organisms. Ed. by J. L. KIRSCHVINK, D. S. JONES, and B. J. MACFADDEN. New York: Plenum Press. 509–533.

MATHER, J. G.; BAKER, R. R. (1981): Magnetic sense of direction in wood mice for route based navigation. Nature **291**, 153–155.

MERMOD, C. (1969): Ecologie et dynamique des populations de trois rongeurs sylvicoles. Mammalia **33**, 1–57.

MEYER DE STADELHOFEN, C.; SIGRIST, W.; DONZÉ, A. (1973): L'anomalie magnétique du Jorat. Bull. Soc. vaud. sc. nat. **71**, 365–371.

PRATT, J. G.; WALLRAFF, H. G. (1958): Zwei-Richtungs-Versuche mit Brieftauben: Langstreckenflüge auf der Nord-Süd-Achse in Westdeutschland. Z. Tierpsychol. **15**, 332–339.

SIEGEL, S. (1956): Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill.

WAGNER, G. (1976): Das Orientierungsverhalten von Brieftauben im erdmagnetisch gestörten Gebiete des Chasseral. Rev. suisse zool. **83**, 883–890.

WAGNER, G. (1983): Natural geomagnetic anomalies and homing in pigeons. Comp. Biochem. Physiol. **76A**, 691–700.

WALCOTT, C. (1978): Anomalies in the earth's magnetic field increase the scatter of pigeons' vanishing bearings. In: Animal migration, navigation and homing. Ed. by K. SCHMIDT-KOENIG and W. T. KEETON. Berlin: Springer Verlag. 143–151.

WESTBY, G. W. M.; PARTRIDGE, K. J. (1986): Human homing: still no evidence despite geomagnetic controls. J. exp. Biol. **120**, 325–331.

WILTSCHKO, W.; WILTSCHKO, R. (1982): The role of outward journey information in the orientation of homing pigeons. In: Avian navigation. Ed. by F. PAPI and H. G. WALLRAFF. Berlin: Springer Verlag. 239–252.

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Activity pattern and thermoregulation in the Cuis
(*Galea musteloides* Meyen, 1833)

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Abstract

Studied basal energetics, thermoregulatory reactions and nycthemeral variation of activity in seven cuis *(Galea musteloides)*. In female animals mean T_{re} was at the same level during day and night (37.3 and 37.4 °C, rsp.). In the males a marked peak was obvious around the transition from L- to D-phase. When exposed to temperatures from 15–35 °C T_{re} was regulated between 36.5–38.5 °C. Exposure to temperatures above 35 °C led to a rapid rise of T_{re}. O_2-consumption was lowest between 30–35 °C; however, BMR in the females was much lower than in the males (0.69 vs 0.94 ml/g·h). This is 17 % below (females) and 15 % above (males) the expected mass-specific value. The increase of O_2-uptake at ambient temperatures below the TNZ was also markedly less in the females. The slope of the regression line was 30 % (females) and 12 % (males) below the calculated mass-specific value for thermal conductance. Measurements of skin temperatures at various parts of the body revealed that in a cold environment heat flow to the periphery was mainly reduced at the tip of the nose and the hind foot pad. Under normal caging conditions activity patterns differed markedly between the sexes: Whereas in the males activity was uniformly distributed over D- and L-phase the females were about twice as active during the night. Additionally, in the female sex a stronger tendency towards longer lasting activity bursts was found.

Introduction

Cuis (vernacular name: pampahuanca) belong to the family Caviidae. The genus *Galea* contains three species which live in two geographically isolated areas (CABRERA 1961; HÜCKINGHAUS 1961): *G. musteloides* has its distribution area in Bolivia and the north-west of Argentina (from 600 to about 4000 m above sealevel) whereas the other two species occur only in the north-eastern parts of Brazil. Although this distribution area belongs to the tropical and subtropical zone, the climatic conditions can be described as temperate. Highest ambient temperatures occur during January with maximal values around 30 °C and lowest temperatures are found during July with the minimum near 0 °C. The area receives rather little rainfall, the bulk of it falling during the hottest month (January).

Although breeding colonies of cuis have been established in a number of laboratories and zoos during the last decade, information about this species is still rather scarce. Investigations have mainly concentrated on sexual and social behaviour (WEIR 1971; TAM 1972; ROOD 1972; ROWLANDS and WEIR 1974). Nothing, however, is known about physiological parameters. As cuis quickly become tame and breed well in captivity they would appear to make an excellent laboratory animal (ROOD 1972). It was the aim of this study, therefore, to obtain some basic values of the energetics and thermal demands of this species. Additionally, the nycthemeral rhythm of activity was investigated.

Material and methods

Seven cuis were used in this study. Two couples (all about one year old) were purchased from the zoos of Zürich and Stuttgart; they gave birth to three young ones in our laboratory. Mean body mass was 330 g in the females and 314.5 g in the males. The cuis were kept as pairs in wooden cages (73 × 73 ×

50 cm) at room temperature 22 $\pm$ 1 °C, relative humidity 50 $\pm$ 5 % and at a L:D-cycle of 12:12 hours. Food consisted of a mixture of sunflower seeds, rolled oats, barley, commercial pellets, yeast powder and minerals. Additionally lettuce, apples and carrots were offered as well as grass, clover and dandelions if available. Occasionally biscuits and crispbread were added. Fresh water was always available.

Rectal temperature (T_{re}) was measured at a depth of 2.5 cm with a thermistor (Ultrakust, Thermophil; accuracy $\pm$ 0.1 °C). To obtain the nycthemeral variation of T_{re} under normal caging conditions not more than four measurements were made during any one day. O_2-consumption and CO_2-production were recorded in an open flow system using analyzers from HARTMANN and BRAUN (Oxytest, Uras). For the measurements the animals were placed in a perspex cylinder ($\emptyset$ 18.7 cm, length 20 cm). Exposure to the various ambient temperatures (T_a) took place in a temperature controlled cabinet (Ehret) where T_a could be regulated to $\pm$ 0.5 °C. Air flow was adjusted to 34.8 l/h (T_a 20–35 °C) and 60.9–69.6 l/h (T_a 15, 37 and 40 °C), respectively. Constancy of air flow was continuously controlled by means of a flowmeter (ROTA). All gas volumes have been corrected to STPD.

Measurements of gaseous exchange were conducted during the second half of the D-phase because T_{re} of the males was lowest during this period. Exposure to the various ambient temperatures lasted for 5 h. At T_a > 35 °C, however, the experiments were disrupted earlier when the animals became restless. Calculation of gaseous exchange started only after an equilibration time of two hours the reported values representing the means over the following period of ca. 3 h. Immediately after opening the respiration chamber T_{re} and body mass were measured.

Skin temperatures (T_s) were obtained with a special surface temperature probe (United Systems Corp., model 581C, 709A). During these experiments the cuis remained in their normal cages and T_a in the room was set to 15, 22 and 34 °C, respectively. Skin temperatures were measured 3 and 7.5 h after changing T_a.

To find out about the nycthemeral variation of locomotor activity the cuis were watched using an infra-red sensitive video-camera (Grundig). Each of the adult couples was observed twice over a complete 24 h period. Length of active and resting periods was registered and occurrence of certain activities noted (e.g. feeding, drinking, grooming, sand-bathing, defecating).

Results

Nycthemeral variations of T_{re}

In the females no obvious diurnal rhythm of T_{re} could be detected (Fig. 1). Mean T_{re} during L-phase and D-phase were nearly identical: 37.3 $\pm$ 0.2 °C vs 37.4 $\pm$ 0.2 °C. A similar situation was found in the males; however, in this sex a marked peak occurred around the time when the lights were switched off in the animal room. Mean T_{re} then was at 38.4 $\pm$ 0.2 °C but dropped to 37.3 $\pm$ 0.2 °C within the next 2 h.

T_{re} after exposure to various ambient temperatures

In both sexes T_{re} was regulated within the normothermic range (36.5–38.5 °C) at ambient temperatures from 15–35 °C (Fig. 2). Exposure to higher T_a led to a rapid rise of T_{re} (to above 41 °C after 50–75 min at T_a 40 °C). Experiments then usually had to be disrupted because the cuis showed signs of severe heat stress (restlessness, defecation, urination).

O_2-consumption at T_a from 15–40 °C

In the females oxygen consumption was markedly lower than in the males over the whole range of tested ambient temperatures (Fig. 3). In both sexes minimal O_2-uptake occurred at T_a from 30–35 °C. Within this thermoneutral zone (TNZ) the basal metabolic rate (BMR) of the females was 17 % below and that of the males 15 % above the mass-specific value as expected after the formula of KLEIBER (1961).

At T_a below 30 °C O_2-consumption increased linearly in the females whereas in the males it showed a more irregular pattern. The increase can be described by the following regression equations:

females: $Y(ml\ O_2/g\cdot h) = 1.795 - 0.038\cdot T_a\ (°C)\ (r = -0.91)$
males: $Y(ml\ O_2/g\cdot h) = 2.493 - 0.049\cdot T_a\ (°C)\ (r = -0.73)$

The slope of the regression lines is 30 % (females) and 12 % (males), respectively, below the calculated mass-specific values after the formula of HERREID and KESSEL (1967). With the exception of $T_a = 15\,°C$ mean values of females and males are significantly different $(p \leqq 0.05)$.

At ambient temperatures above the TNZ O_2-consumption increased only moderately.

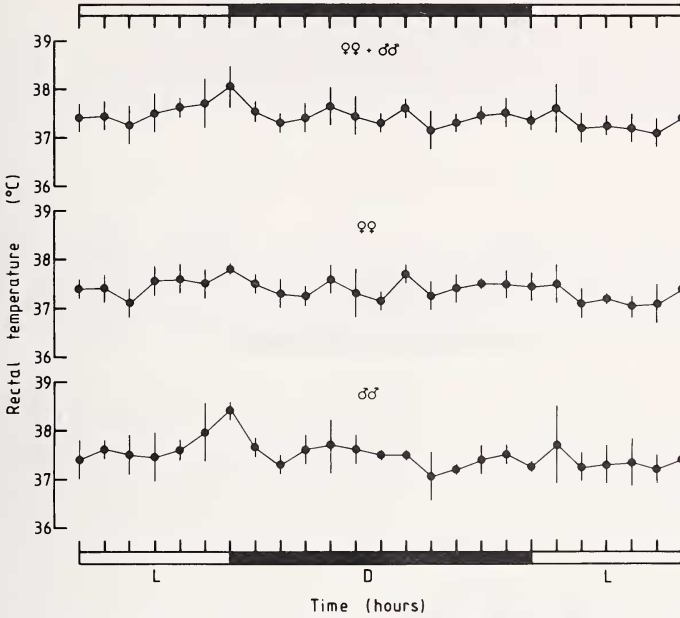Fig. 1. Nycthemeral variation of rectal temperature (mean values ± S.D.) in cuis (3 males, 4 females). Each animal was measured twice at every full hour
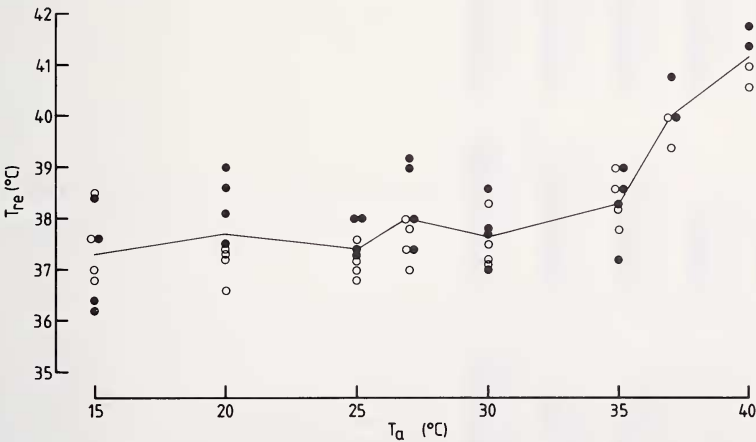

Fig. 2. Rectal temperature after exposure to ambient temperatures from 15–40 °C. Exposure lasted for five hours except for ambient temperatures above 35 °C when experiments were disrupted earlier to spare the animals. Empty circles = females, filled circles = males; the line represents the mean value of both sexes
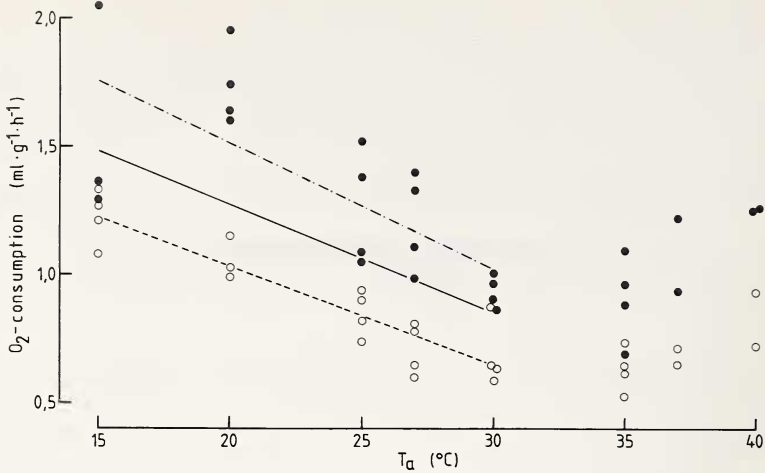
Fig. 3. Oxygen uptake at ambient temperatures from 15–40 °C (calculated mean after an equilibration time of ca. 2 hours; empty circles = females, filled circles = males). Lines represent regression lines for the increase of O_2-consumption at temperatures below the TNZ: ------ = ♀♀: Y (ml O_2/g·h) = 1,795 – 0,038·T_a (°C); r = −0,91; ·––·– = ♂♂: Y (ml O_2/g·h) = 2,493 – 0,049·T_a (°C); r = −0,73; —— = ♀+♂: Y (ml O_2/g·h) = 2,111 – 0,042·T_a (°C); r = −0,61

T_{re} and T_s at different ambient temperatures under normal caging conditions

In five cuis (3 females, 2 males) we measured T_{re} and T_s at various sites of the body (naked spot above sternal region, inner side of earlaps, hind foot pad, tip of the nose) after exposure to ambient temperatures 15, 22 and 34 °C, respectively (Fig. 4). During these experiments the animals were kept in pairs in their normal cages. After 7.5 h T_{re} and T_s
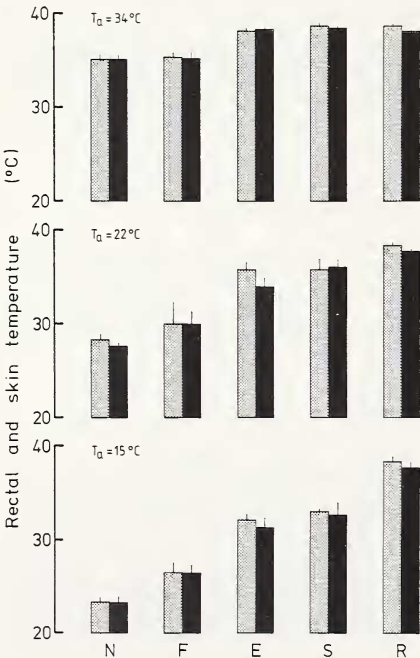

Fig. 4. Skin temperatures at the tip of the nose (N), hind foot pad (F), inner side of earlap (E) and bare patch over sternal region (S) after 3 (left column) and 7 (right column) hours of exposure to ambient temperatures 15, 22 and 34 °C. R = rectal temperature. Height of columns indicates mean value, line indicates S.D. (n = 5; 3 females, 2 males)

were not significantly different from those after 3 hours exposure. At all tested ambient temperatures T_s was lowest at the tip of the nose. The skin temperature of the sternal region and of the earlaps always remained above 30 °C. It fell below this level at the tip of the nose at T_a 22 °C and, additionally, at the hind foot pad at T_a 15 °C suggesting an energy saving reduction of the heatflow to these parts of the body at lower ambient temperatures.
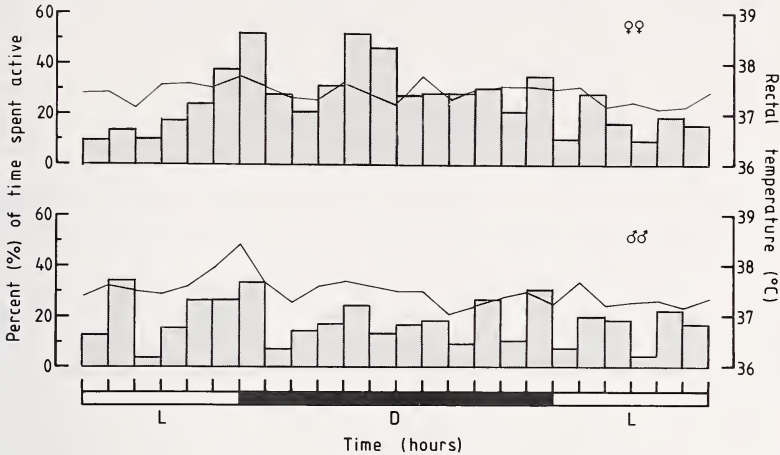

Fig. 5. Nycthemeral variation of time spent active. Mean values calculated for periods of 60 min. The animals were observed with an infrared video device in their normal cages. Each couple was watched twice for a full 24 h period. Lines represent nycthemeral variation of rectal temperature (see Fig. 1)
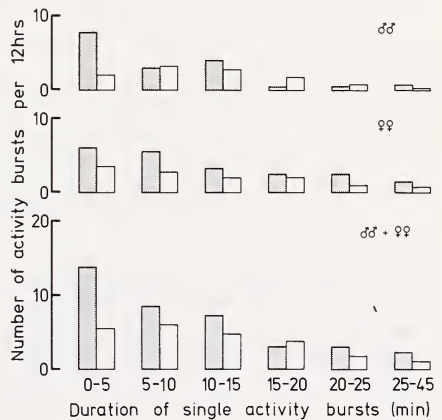

Fig. 6. Relationship between frequency and duration of single activity bursts during D-phase (dotted columns) and L-phase (empty columns)

Activity pattern under normal caging conditions

In the males no obvious nycthemeral variation of the activity pattern could be detected (Fig. 5). Periods of increased activity were rather uniformly distributed over L- and D-phase. If at all, longer lasting periods of increased activity in the male sex occurred before and shortly after switching the lights off and then again during the first half of the D-phase.

The females, on the other hand, showed a different pattern of activity: Two marked peaks occurred at the beginning and at the end of the first half of the D-phase. Whereas the activity level remained fairly high throughout the whole D-phase it was markedly lower

when the lights were on. During the L-phase both sexes spent about the same time active (17.4 % and 17.5 %, respectively). During the D-phase, however, activity increased to 32.9 % of the total time in the females and to only 18.5 % in the males.

Durations of single activity bursts were also somewhat different in both sexes (Fig. 6). Whereas the males preferably were active for periods shorter than 15 min (with a clear maximum of activity bursts ≦ 5 min during the D-phase) the females showed a much stronger tendency for extended periods of activity (duration ≧ 15 min). Visual observation revealed that almost any activity burst was accompanied by the intake of food. Drinking, on the other hand, was almost never seen.

Discussion

The most striking results of our investigations certainly are the marked sexual differences in the level of heat production and in the pattern of daily activity. As yet it is unclear why the basal metabolic rate of female cuis is much lower than that of males (0.69 vs 0.94 ml O_2/g·h at T_a 30 °C). It must be emphasized that this difference in heat production was found at all tested ambient temperatures although rectal temperatures differed only slightly between the sexes.

Sexual differences in heat production have also been reported for a gerbil, *Gerbillus perpallidus* (MÜLLER 1985). However, in this desert species BMR was lower in the male sex which, additionally, had also a lower rectal temperature. Reliable information about different levels of heat production among the sexes of other species is unfortunately missing. One can, therefore, only speculate if the peculiarities in the energetics of gerbils and cuis are related to their different reproductive strategies. The higher levels of heat production and rectal temperature in the females of the altricial gerbils could allow a relatively faster development of the young ones during the prenatal period.

The differences in the energetics of female and male cuis are probably also reflected in their different activity patterns. Our observations revealed that female cuis spend substantially more time active than males, the increased activity almost entirely occurring during the D-phase. It seems possible that the lower basal heat production in the females is an adaptation to keep their daily energy expenditure at a level similar to that of the males in spite of their increased activity. This view is again corroborated by findings in *Gerbillus perpallidus* where preliminary results suggest a lower level of activity in the females which – in this species – show a higher rate of basal heat production than males (MÜLLER 1985 and unpubl. observ.).

Our results indicate a clearly polyphasic activity pattern of cuis in both sexes. Activity bursts occur distributed over the entire 24 hours period. As stated above, however, the females are almost twice as active during the night than during the day. This finding is contradictory to ROOD's (1972) and WEIR's (1972) observations. These authors classify cuis as being day-active. However, ROOD watched his animals only for two hours in the morning and again in the evening. This limited observation time probably does not allow to obtain a detached view of the entire nycthemeral rhythm. Measuring the composition of the urine, on the other hand, BELLAMY and WEIR (1971) concluded that cuis should be night-active. From the data available at the moment it seems most probably that cuis are polyphasic with a rather uniformly distributed activity in the males (with a small peak around the transition from L-phase to D-phase) and a clear accentuation of activity during the D-phase in the females.

A comparison of our results with those obtained from guinea pigs is rendered difficult because investigations in this species have either only been made with males or the authors do not state the sex of their animals. However, as pointed out above there may exist marked differences between the sexes with regard to activity levels, activity patterns and